Subterranean Biology 53: 1–11 (2025)
doi: 10.3897/subtbiol.53.161945
https://subtbiol.pensoft.net

RESEARCH ARTICLE

A peer-reviewed open-access journal
Subterranean Biology
Published by The International Society for Subterranean Biology

NOR and C-heterochromatin characteristics of *Ellobius lutescens* Thomas, 1897 (Rodentia, Cricetidae) from Turkey

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Academic editor: Peter Trontelj | Received 12 June 2025 | Accepted 22 July 2025 | Published 11 August 2025

https://zoobank.org/61869847-7860-41B7-AE6B-DCD97353D9CE

Citation: Yürümez G (2025) NOR and C-heterochromatin characteristics of *Ellobius lutescens* Thomas, 1897 (Rodentia, Cricetidae) from Turkey. Subterranean Biology 53: 1–11. https://doi.org/10.3897/subtbiol.53.161945

Abstract

The genus *Ellobius* Fischer, 1814, adapted to subterranean life, consists of five species distributed in the Palaearctic region and only *Ellobius lutescens* Thomas, 1897 occurs in Turkey. Although karyological, morphological, and biological studies have been conducted on populations of this species in Turkey, there is no study focused on nucleolar organizer regions (NORs) or C-heterochromatin characteristics. Nine specimens (five females and four males) were collected from four different localities in Van and Hakkâri provinces in Eastern Anatolia in this study. Cytogenetic analyses on these specimens confirmed a conserved diploid number (2n = 17) and the unusual sex chromosome system (XO in both sexes). An interstitial NOR on chromosome 1 and numerous telomeric NORs on the other chromosomes were detected by silver nitrate staining. In addition, C-banding analyses detected no C-band heterochromatin in any of the chromosomes, including the X. These cytogenetic results, along with current morphometric and genetic data, indicate subspecies-level variation between Turkish and Iranian populations, emphasizing the influence of physical barriers on micro-evolutionary divergence. This study is the first investigation of NORs and C-heterochromatin in Turkish populations of the subterranean rodent *E. lutescens* to date. In addition, our study expands the southernmost distribution limit of this species up to Karabey village (Yüksekova-Hakkâri) in Turkey.

Keywords

C-heterochromatin, cytogenetics, *Ellobius lutescens*, NOR, Turkey

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Introduction

The genus *Ellobius* Fischer, 1814, belongs to the family Cricetidae and comprises five recognized species (*E. talpinus* (Pallas, 1770), *E. tancrei* (Blasius, 1884), *E. alaicus* (Vorontsov et al., 1969), *E. fuscocapillus* (Blyth, 1843) and *E. lutescens* Thomas, 1897). The genus *Ellobius* exhibits an allopatric distribution that extends from Ukraine across Central Asia to Kazakhstan, Mongolia, and China, as well as into eastern Turkey and Iran (Panteleyev 1998; Coşkun 2001, 2016; Musser and Carleton 2005; Batsaikhan and Tinnin 2016; Gerrie and Kennerley 2016; Kryštufek and Shenbrot 2016; Rusin 2016; Wilson et al. 2017; Kaya et al. 2018; Lebedev et al. 2020).

The genus *Ellobius* (excluding *E. fuscocapillus*) exhibits an exceptionally rare pattern of sex chromosome differentiation among mammals, making it a subject of significant interest in cytogenetics. *Ellobius talpinus* has a diploid number of 2n = 54 and possesses isomorphic sex chromosomes (XX in both sexes). *E. tancrei* (2n = 54) and *E. alaicus* (2n = 52) have XX configurations in both sexes, with one X chromosome functionally inactive. In contrast, *E. lutescens* is characterized by a highly unusual karyotype, with a diploid number of 2n = 17 and an XO sex chromosome system present in both males and females —a rare phenomenon in mammals (Vorontsov et al. 1969; Lyapunova and Vorontsov 1978; Borisov et al. 1991; Kolomiets et al. 1991; Bakloushinskaya and Lyapunova 2003; Bakloushinskaya et al. 2012).

Ellobius lutescens, commonly known as the Transcaucasian mole vole, was first described by Thomas (1897) based on specimens collected from Erçek near Van in eastern Turkey. However, the taxonomic status of this species was debated for many years. Several researchers have classified these specimens as either *E. fusco-capillus* (Walker 1964; Hassinger 1973; Kumerloeve 1975; Roberts 1977; Corbet 1978; Morlok 1978; Doğramacı 1989; Harrison and Bates 1991) or as a subspecies thereof (Ognev 1950; Lay 1967), while others have maintained that *E. lutescens* and *E. fuscocapillus* are distinct species, and that the species occurring in Anatolia is *E. lutescens* (Neuhauser 1936; Vinogradov and Argiropulo 1941; Ellerman 1941, 1948; Ellerman and Morisson-Scoot 1951; Osborn 1962; Çağlar 1967; Corbet and Hill 1991; Coşkun 1997, 2001; Coşkun and Ulutürk 2003; Kaya and Coşkun 2015; Coşkun 2016). The most current consensus recognizes a single species of the genus *Ellobius*, *E. lutescens* Thomas 1897, is distributed in Turkey (Coşkun 1997, 2001; Coşkun and Ulutürk 2003).

Ellobius lutescens, a Palaearctic rodent species, is distributed across northwestern Georgia, Iran, Azerbaijan, Armenia, and eastern Turkey (Thomas 1897; Ellerman and Morrison-Scott 1951; Osborn 1962; Corbet and Hill 1991; Coşkun 1997; Nowak 1999; Wilson and Reeder 2005; Kryštufek and Shenbrot 2016; Wilson et al. 2017). Within Turkey, *E. lutescens* is the only representative of the genus *Ellobius*, with confirmed populations confined to the eastern part of the country (Coşkun 1997, 2001; Coşkun and Ulutürk 2003; Gharkheloo and Kıvanç 2003; Kaya and Coşkun 2015; Coşkun 2016) (Fig. 1).

Figure 1. *Ellobius lutescens* specimen from Karabey village, Turkey.

This species inhabits semi-deserts, grasslands, and steppes in Turkey, and is adapted to subterranean life with its specialized burrowing ability (Kryštufek and Vohralík 2009; Coşkun 2016).

Ellobius lutescens, typically dig their own burrows, which consist of multiple interconnected chambers and extensive tunnel systems (Coşkun 2001). The depth of these burrow systems ranges from 16 cm to 48 cm below ground, depending on surface climatic conditions. The tunnel systems are highly complex, with each family occupying a living area of approximately 12 m × 9 m (Coşkun and Ulutürk 2003).

The uniformity of the subterranean environment has caused the *E. lutescens* to acquire morphological (e.g., cylindrical body, short limbs, absence of external ear pinnae, soft and short fur, extremely small eyes, and a very short tail) and physiological (e.g., strong muscles for digging, tolerance to low oxygen (hypoxia) and high carbon dioxide (hypercapnia) levels, and high sensitivity to soil vibrations) adaptations suitable for subterranean life (Coşkun 2001).

The first cytogenetic study of *E. lutescens* was carried out by Matthey (1953) on Iranian specimens and reported that both male and female specimens had a diploid chromosome number of 2n = 17. Later karyological studies performed by different researchers (Hsu and Benirschke 1969; Voronstov et al. 1969; Zima and Kral 1984; Borisov et al. 1991; Coşkun 1997; Gharkheloo and Kıvanç 2003; Graphodatsky et al. 2011)

confirmed the diploid chromosome number (2n)=17, fundamental number (NF)=34, fundamental autosomal number (NFa)=32, and XO in both males and females.

The taxonomic, karyological, morphological, and some biological characteristics of *E. lutescens* have been investigated in different localities of Turkey by Coşkun (1997, 2000, 2001) and Coşkun and Ulutürk (2003) (Fig. 2). However, studies focusing on the nucleolar organizer regions (NORs) and C-heterochromatin characteristics of this species are limited. To date, NOR staining and C- heterochromatin characteristics of this species have only been reported by Djalali et al. (1986) and Vogel et al. (1988), respectively, in the Tehran (Iran) population.

The first karyological study on *E. lutescens* in Turkey was carried out by Coşkun (1997) and reported that the diploid chromosome number in both sexes was 2n = 17. In recent years, studies have been carried out in various fields related to this species. Ellerman (1948) compared the external morphological characteristics of *E. lutescens* specimens from Van (Turkey) and Dumbeneh (Iran). Kaya et al. (2018) conducted the first geometric morphometric analysis on the cranial morphology of *E. lutescens* specimens obtained from Iran and Turkey. In addition, Alireza et al. (2018) investigated the population genetic structure of *E. lutescens* distributed along the Zagros Mountains in Iran. Although the presence of this species is known in eastern Anatolia in Turkey, its detailed cytogenetic peculiarities — particularly banding patterns— have not yet been documented. So far only conventional karyotype peculiarities have been reported for the Turkey population; no studies have been conducted on the distribution of C-heterochromatin and NOR patterns.

The aim of this study was to reveal the NOR patterns and C-heterochromatin peculiarities of *E. lutescens* specimens collected from Turkey.

Methods

A total of nine *E. lutescens* specimens (five females and four males) were collected from four localities in eastern Turkey: Keçikıran (38°57.83'N, 43°37.55'E), Çolpan (38°53.76'N, 43°33.40'E) and Saray (38°40.15'N, 44°8.90'E) (Van province) and Karabey (37°26.34'N, 44°25.37'E) (Yüksekova district, Hakkâri province) (Fig. 2).

Chromosome preparations were obtained from colchicine-treated bone marrow cells, according to Ford and Hamerton (1956). At least 20 well-spread metaphases per specimen were analysed. For NOR detection, slides were silver-stained following Howell and Black (1980). The C-banding was performed using the technique reported by Sumner (1972).

Results

Karyological peculiarities of 2n = 17, NF = 34, and NFa = 32 were detected in all analyzed samples of *E. lutescens*. The karyotypes of both males and females were comprised of eight pairs of biarmed (metacentric or submetacentric) autosomes and a single biarmed sex chromosome. Both sexes displayed an XO chromosome constitution, with no identifiable Y chromosome (Fig. 3).

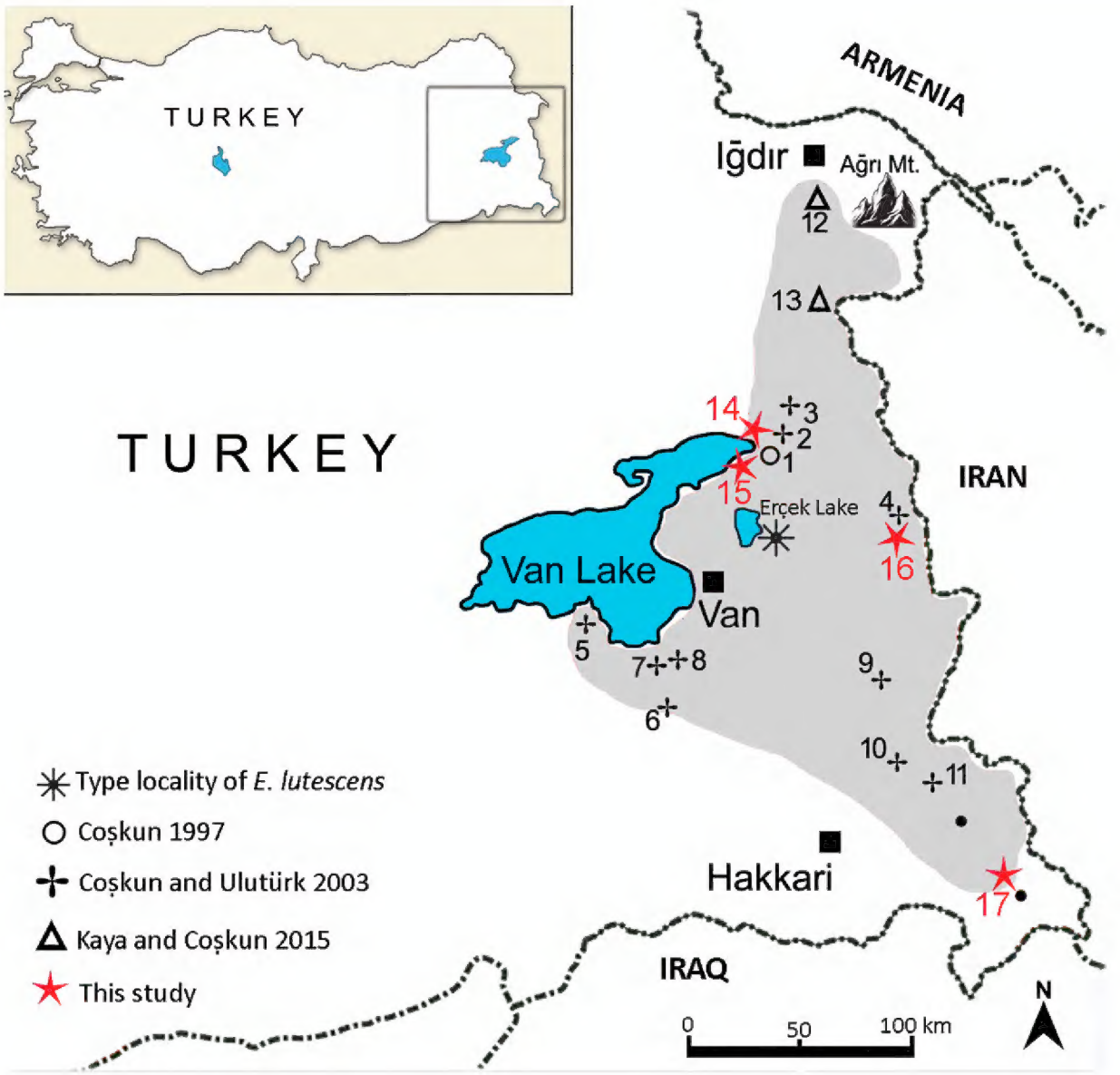

Figure 2. Collected localities of *E. lutescens* and previous studies from Turkey (1.Van-Ovapınar (Çoşkun 1997); 2. Van-Muradiye-Balıklı village, 3. Van-Muradiye-Gönderme village, 4. Van-Saray, 5.Van-Gevaş-Güzelkonak village, 6. Van-Çatak-Kayaboğazı village, 7. Van-Gürpınar-Köprüler village, 8. Van-Çatak-Köklü village, 9. Van-Başkale, 10. Hakkâri- Yüksekova-Hanemusa village, 11. Hakkâri-Yüksekova-Suüstü village (Coşkun and Ulutürk 2003); 12. Iğdır (23 km S), 13. Ağrı-Doğubayazıt-Çetenli (Kaya and Coşkun 2015); 14. Van-Muradiye-Keçikıran village, 15. Van-Tuşba-Çolpan, 16. Van-Saray, 17. Hakkâri-Yüksekova-Karabey village (This study).

Silver nitrate staining revealed distinct NORs at multiple chromosomal loci. Interstitial NORs were observed on the long arm of one homologue (chromosome pair no. 1). While NORs were localized at the telomeric regions of the short arms of single homologues (chromosome pairs 2 and 3), other NOR signals were detected on the short arms of both homologues (chromosome pairs 4), and on the long arms of both homologues (chromosome pairs 5 and 7). No NOR signal was detected on the X chromosome (Fig. 4).

No C-banding was detected in any of the chromosome preparations from all examined specimens of *E. lutescens* (Fig. 5).

The southernmost distribution of *E. lutescens* in Turkey was recorded as Karabey Village (37°26.34'N, 44°25.37'E, 1870 m asl.) in the Yüksekova District of Hakkâri Province. No burrow systems or mounds were detected during field surveys conducted further south of this locality.

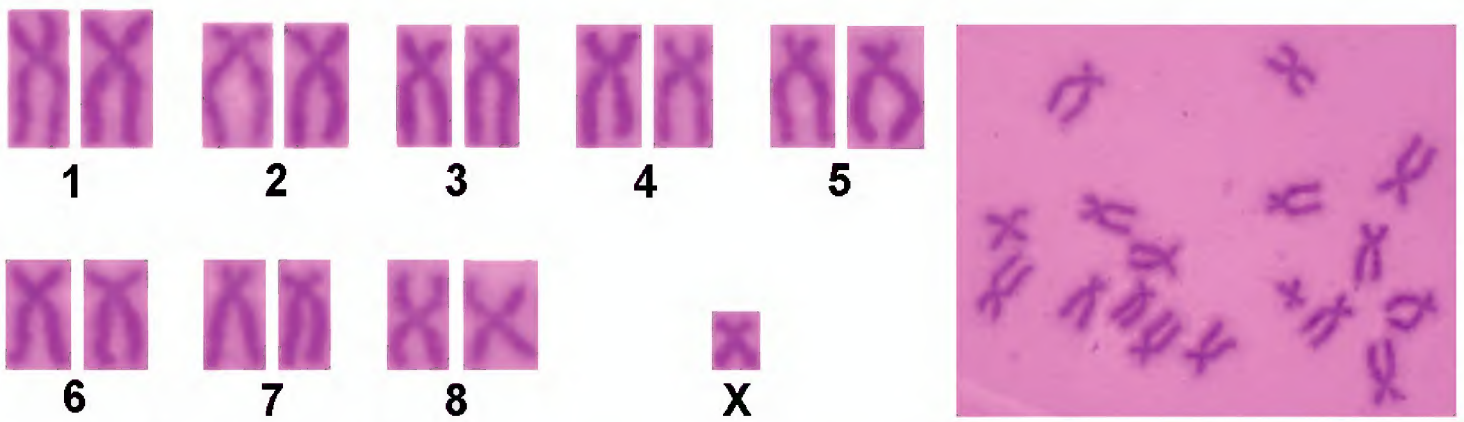

Figure 3. Mitotic metaphase spread and conventional karyotype of *E. lutescens*.

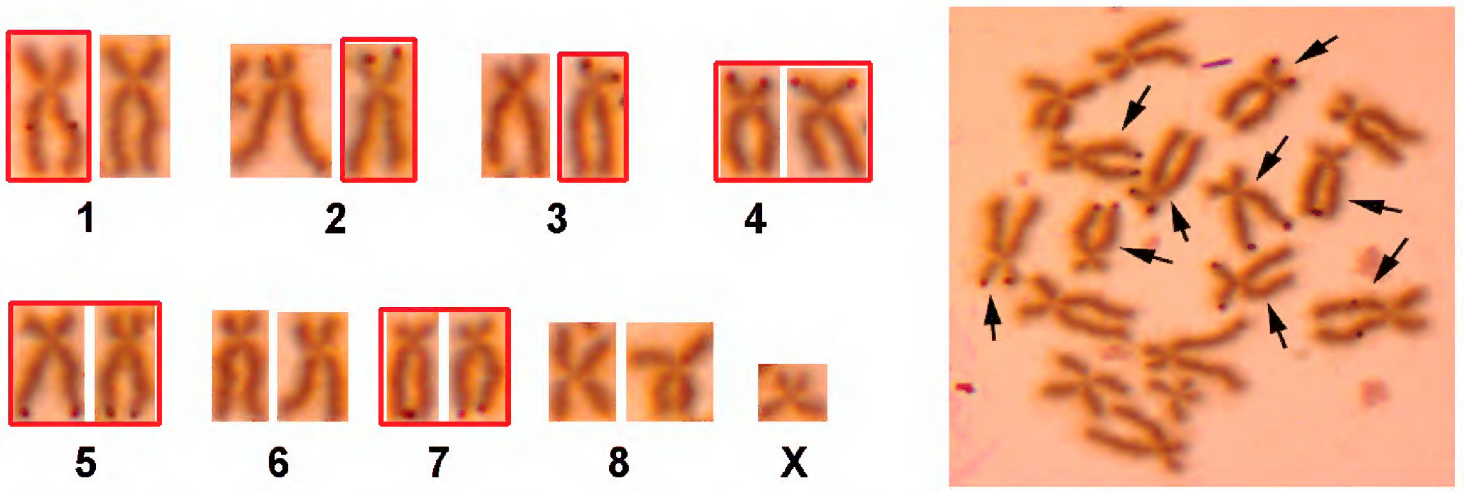

Figure 4. The silver-stained metaphase spread and karyotype of *E. lutescens*.

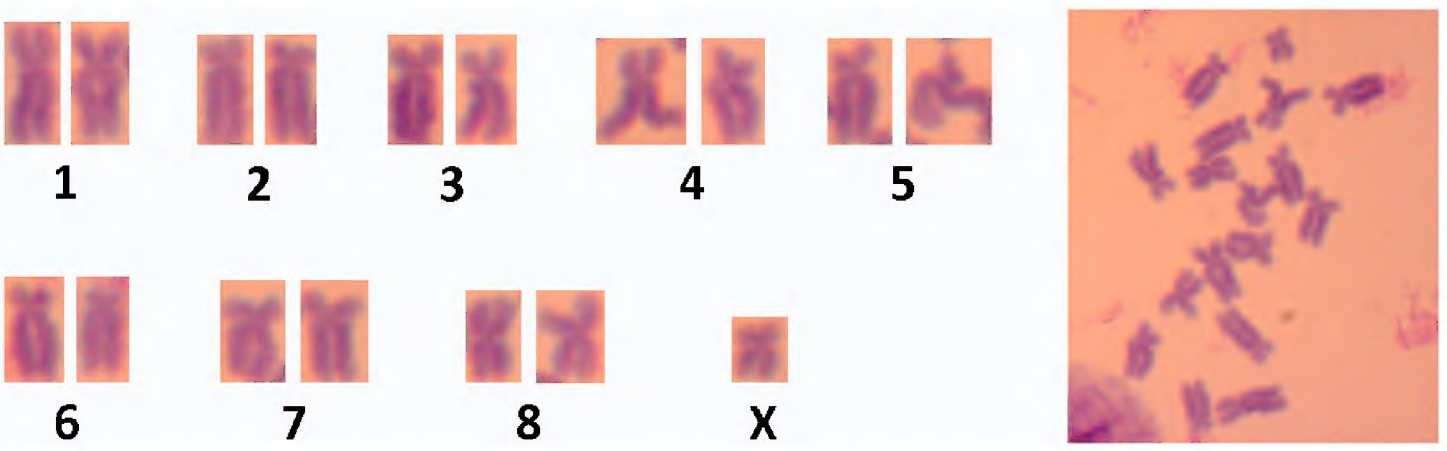

Figure 5. The C-banded metaphase spread and karyotype of *E. lutescens*.

Discussion

The karyological characteristics of *E. lutescens* are unique among mammals. The most remarkable features of this species are that its diploid chromosome numbers are odd (2n = 17), and the sex chromosome constitution of both sexes is XO (Matthey 1953, 1957; Hsu and Benirschke 1969; Vorontsov et al. 1969; Zima and Kral 1984; Coşkun 1997; Gharkheloo and Kıvanç 2003; Graphodatsky et al. 2011).

When all the studies (Mathey 1953, 1957; Hsu and Benirschke 1969; Voronstov et al. 1969; Lyapunova et al. 1980; Zima and Kral 1984; Djalali et al. 1986; Borisov

et al. 1991; Coşkun 1997, 2001; Coşkun and Ulutürk 2003; Gharkheloo and Kıvanç 2003; Graphodatsky et al. 2011; Coşkun 2016, and the present study) on samples obtained from various regions of the distribution area of *E. lutescens* were evaluated, it was determined that all populations of *E. lutescens* exhibited stability of the chromosome number (2n = 17), morphology (NF = 34, NFa = 32, and sex chromosomes (XO in both sexes). The significant evolutionary changes from (XX, XY) to (XO) types in both male and female sex chromosomes of *E. lutescens* indicate that it occupies a special position among mammals whose sex chromosome systems are typically dimorphic (XX/XY) (Borisov et al. 1991; Kolomiets et al. 1991; Bakloushinskaya and Lyapunova 2003). Unfortunately, little is known about the molecular basis of sex determination in these animals (Baumstark et al. 2005; Just et al. 2007; Bakloushinskaya 2009; Bakloushinskaya and Matveevsky 2018).

Cytogenetic data such as C-heterochromatin and NORs are widely used in intra- and interspecific chromosomal variation, particularly among closely related species (Arslan et al. 2011; Zhu et al. 2019). These markers provide important insights into chromosomal organization, evolutionary divergence, and species/subspecies differentiation.

Djalali et al. (1986) reported in the specimens of *E. lutescens* from Tehran (Iran) province that interstitial NORs are localized on the long arms of the two biarmed chromosomes (no. 1 and 2), besides four chromosomes that have NORs at the telomeres. *E. lutescens* specimens from Turkey have interstitial NORs are localized on the long arm of a biarmed chromosome (no. 1) additionally; NORs are also localized on the terminal of eight chromosomes (Fig. 4). The number of chromosomes with NORs in our specimens from Turkey was found to be significantly higher than the number reported by Djalali et al. (1986) from Tehran (Iran).

Vogel et al. (1988) reported the absence of C-bands in *E. lutescens* chromosomes from Tehran (Iran). Similarly, all examined *E. lutescens* specimens from Turkey exhibited C-negative signals, indicating the absence of detectable constitutive heterochromatin using the C-banding technique. Findings of the present study are consistent with the C-banding findings of Vogel et al. (1988). However, the present study differs significantly in the number and localization of NORs, suggesting population-specific cytogenetic variation between the Iranian and Turkish *E. lutescens* populations.

Kaya et al. (2018) reported that clear morphological divergence in skull and mandible shape between Iranian and Turkish *E. lutescens* populations, proposing that the Zagros and Tendürek mountain ranges serve as significant geographical barriers contributing to subspecies-level separation. Similarly, Alireza et al. (2018) revealed evolutionary divergence within Iranian populations, identifying two evolutionary units along the northern and southern slopes of the Zagros Mountains.

Ellerman (1948) stated that *E. lutescens*, described by Thomas (1897) in Van (Turkey), was *E. l. lutescens*; additionally, *E. woosnami*, described by Thomas (1905) in Dumbeneh (Iran), was *E. l. woosnami*. Current morphological (Kaya et al. 2018) and genetic (Alireza et al. 2018) data, when combined with the cytogenetic data presented in this study, provide compelling cytogenetic evidence of population-level differentiation between the *E. lutes-*

cens populations in Turkey and Iran, and support the existence of subspecies-level micro-evolutionary differentiations between these two populations. All these results supports that the view of Ellerman (1948) that the *E. lutescens* population in Turkey is the subspecies *E. l. lutescens* while the population in Iran is the subspecies *E. l. woosnami* and indicate significant evolutionary and geographic differentiation within the species.

In conclusion, this study presents the first comprehensive cytogenetic analysis of NORs and C-heterochromatin in *E. lutescens* populations from Turkey. Our findings confirm the species' distinctive chromosomal configuration (2n = 17, XO in both sexes) and reveal a higher number of NOR-bearing chromosomes and a more varied NOR localization pattern compared to previously studied Iranian populations.

Absence of detectable C-heterochromatin combined with the numerous and varied NOR distribution provides compelling cytogenetic evidence for population-level divergence. When integrated with previous morphological and genetic data, these results support the classification of the Anatolian population as a distinct subspecies (*E. l. lutescens*). Additionally, this study updates the known distribution range of *E. lutescens* in Turkey, identifying Karabey (Yüksekova, Hakkâri Province) as the species' southernmost limit.

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